NEUROSCIENCE AND THE LAW — SCIENCE AND SOCIETY

The neuroscience of memory: implications for the courtroom

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Abstract | Although memory can be hazy at times, it is often assumed that memories of violent or otherwise stressful events are so well encoded that they are effectively indelible and that confidently retrieved memories are almost certainly accurate. However, findings from basic psychological research and neuroscience studies indicate that memory is a reconstructive process that is susceptible to distortion. In the courtroom, even minor memory distortions can have severe consequences that are partly driven by common misunderstandings about memory — for example, that memory is more veridical than it may actually be.

Pioneers in neuroscience such as Ramón y Cajal, Hebb and Marr introduced the idea that memory is encoded in the patterns of synaptic connectivity between neurons. Changes in the strengths of these synapses encode our experiences and thereby shape our future behaviour. Our understanding of the complex mechanisms that underlie learning and memory has progressed dramatically in recent decades, and studies have not provided evidence that memories are indelible. Quite the contrary, it is becoming clear that there are several ways through which memories can change.

The 'imperfection' of memory has been known since the first empirical memory experiments by Ebbinghaus[1], whose famous 'forgetting curve' revealed that people are unable to retrieve roughly 50% of information 1 hour after encoding. In addition to simple forgetting, memories routinely become distorted[2–7]. The public perception of memory, however, is typically that memory is akin to a video recorder[8] (BOX 1). This distinction between the perception and reality of memory has important consequences in the context of the courtroom. In the legal system, like among the general public, it is generally assumed that memory is highly accurate and largely indelible, at least in the case of 'strong' memories.

The fallibility of memory obviously has implications for the question of how much weight should be given to eyewitness testimony in court cases. Recently, some regional jurisdictions in the United States, such as New Jersey[9,10], Massachusetts[11], Texas[12] and North Carolina[13], have implemented procedural changes designed to mitigate effects of memory biases and to preserve accurate memories of eyewitnesses as well as possible. However, the legal system writ large has been slow to adapt to research findings on memory, even though these findings have implications not only for eyewitness testimony but also for how jurors remember and weigh evidence. Interest in research on memory processes and their relevance to the courtroom has increased since the advent of DNA evidence, which has exonerated hundreds of individuals who were falsely convicted on the basis of eyewitness testimony.

Common misunderstandings

In many countries, the justice system relies on judges or jurors weighing evidence from multiple sources with varying levels of credibility. The belief that a confident memory is always highly accurate and resistant to distortion or loss is an unfortunate misunderstanding about memory[8] that has important consequences in court. The testimony of eyewitnesses whose memories may have been distorted can lead to the conviction of innocent people while true perpetrators remain free. The Innocence Project in New York City, USA (BOX 2), which advocates the use of DNA testing to exonerate wrongfully convicted people, lists 310 exonerated individuals (as of 8 July 2013). These individuals were typically convicted on the basis of eyewitness testimony and spent an average of 13.6 years in confinement before being released. They are thought to be only a small sample of the total number of wrongfully convicted people, as DNA evidence is only available in a limited number of cases (for example, those involving sexual assault).

Most individuals outside the field of memory research (including jurors) are largely unaware of the substantial malleability of memory[2,8,14–16] (however, also see REF. 17). Early studies on the public awareness of memory phenomena showed that when college students were asked how various factors influence memory (for example, cross-race identification, stress and the wording of questions), they were only 54% correct[2]. Although the students scored higher than chance, the score was surprisingly low considering the implications of these factors in court cases. Similar surveys have replicated these findings in non-traditional (that is, older, working) students and in citizens of Washington DC, USA. In both of these studies, the respondents' accuracy was below 50%, suggesting that college students may be slightly better informed about factors that influence memory than the general public[14].

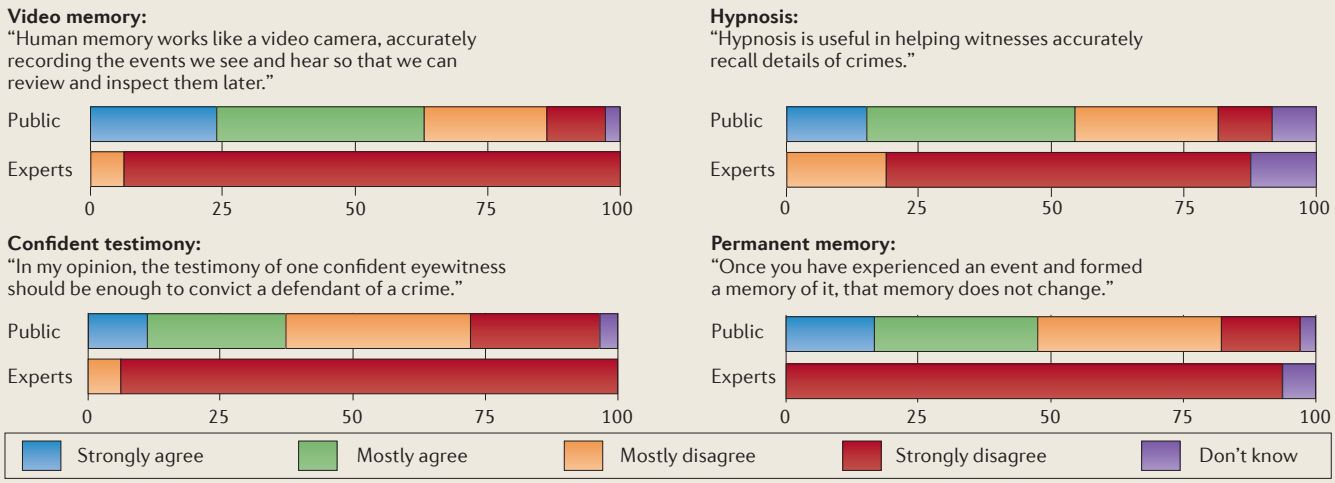
More recent studies revealed that judges and law enforcement personnel are not much more aware of memory phenomena than are college students[16]. For example, on a 30-item questionnaire about memory-related topics, potential jurors (that is, citizens who have been summoned to jury duty), judges and law enforcement personnel (including detectives, police officers and special agents) responded differently from eyewitness testimony experts on 87%, 60% and 60% of items, respectively[16]. Thus, although judges and law enforcement personnel agreed with memory experts on more statements regarding memory myths than did jurors, their understanding of most memory myths still differed from that of memory experts. There is evidence that some populations, such as a surveyed sample of Canadian citizens, hold beliefs that are more in line with those of experts[17]. However, the most recent studies show that there remains a large discrepancy between public knowledge of memory and expert consensus[8] (BOX 1).

One memory phenomenon of which the general public (and therefore also juries) is often unaware is cross-race bias[16,18] — a reduction in accuracy when identifying faces of a race or ethnic background that is different from one's own[2,19]. This phenomenon is due to the fact that we use our entire existing body of knowledge and experiences to filter what we perceive, attend to and use in memory reconstruction (this is known as memory's 'bias' (REF. 20)). In the case of facial identification, we may often be most familiar and knowledgeable about the facial features of our own race and less so of other races or ethnic backgrounds owing to a simple lack of experience with faces of other races (such experience can reduce or eliminate the effect).

Bartlett[21] first drew attention to memory's 'bias' in his famous study on the War of the Ghosts, in which participants had difficulty

Box 1 | **Is memory common sense? Public opinion versus memory experts**

When asked about statements regarding memory-related phenomena in a national survey across the United States, members of the general public (n = 1,500) accepted many phenomena that were not endorsed by experts in the field (that is, professors with more than 10 years of experience in memory research), who showed strong consensus among themselves (see the figure)[8]. Such misunderstandings of memory can have significant consequences in court, where judges and jurors often assume memory to be more accurate and veridical than is indicated by the neurobiologically reconstructive nature of memory. Note that one limitation of these surveys is that expert opinion about memory-related phenomena may change over time as more research findings become available. For example, a 1989 study[15] showed that expert opinion regarding the phenomenon of weapon focus had changed compared with a survey published in 1982 (REF. 14), and further changes in expert opinion regarding weapon focus as well as other phenomena were shown in 2001 (REF. 18). Although expert opinion about memory-related phenomena may sometimes be wrong, it is presumably the best indication of the true nature of such phenomena. The authors of one recent study[17] suggested that public opinion and expert opinion are beginning to converge. However, other studies suggest that, in some aspects, lay beliefs are still quite different from those of experts. There is, therefore, a need for periodic updating of both expert and public opinion. Data from REF. 8.



recalling short stories word for word when the stories did not fit into their conceptual framework. Barlett's work was later developed by Neisser[22], who famously likened memory retrieval to palaeontology by saying, "out of a few stored bone chips, we remember a dinosaur". Put simply, if we think an event should have happened in a certain way on the basis of our previous experiences, we are likely to think that the event did indeed happen this way. For example, when people read a brief passage about a wild and unruly girl and are told that it is about Helen Keller, they are more likely to mistakenly remember, a week later, the text saying 'she was deaf, dumb and blind' than if they were told that the passage is about a fictitious Carol Harris[23]. Thus, if people expect certain things to occur during a crime or expect a particular group of people to be more or less involved in crimes, it should perhaps not come as a surprise that their memories reflect these biases.

Another commonly held belief among the general public is that an eyewitness's confidence in the accuracy of his or her memory is a strong indicator of the actual accuracy of the memory[16]. Jurors often place great weight on how confident an eyewitness is regarding their memory of the event — enough to convict an individual even if eyewitness testimony is the only condemning evidence (BOX 1). Meta-analyses have reported that mistaken eyewitness identification occurred in 75% or more of cases in which a convicted individual was later exonerated on the basis of DNA evidence[24]. Importantly, memory experts generally do not endorse the idea that the confidence and accuracy of a memory are always tightly linked[8,18]. Although studies in cognitive psychology have shown a positive correlation between memory confidence and accuracy[25,26], these studies were typically laboratory-based, used neutral stimuli, and observed general memory phenomena rather than the attributes of memory that are most relevant to court. Research that specifically examines eyewitness testimony or the memory of traumatic events has shown weak[27] or even negative[6] correlations between a person's confidence in the accuracy of a memory and the actual accuracy of that memory. One reason for these weak correlations is that confidence can be influenced independently of accuracy: for example, by post-identification feedback, which has no influence on accuracy (see below). Such decoupling between memory confidence and accuracy can be seen when college students or law enforcement personnel are given instructions on how to detect behavioural cues of deception. This lie detection training tends to increase confidence in evaluating whether a witness's testimony is truthful or deceitful without necessarily improving the actual accuracy of deception detection[28–30]. Thus, the relationship between confidence and accuracy is far more complicated than is often acknowledged. Accuracy often produces confidence, but confidence does not necessarily indicate accuracy.

Misunderstandings about memory can have effects on criminal cases even before they make it to court. The belief that confident, detailed memories are always accurate and reliable is contrary to research that suggests the opposite is possible — confidently recalled recollections can sometimes be inaccurate, and real memories are not always highly confident and detailed. Especially in cases involving violence and high levels of stress, real traumatic memories — which can be disjointed — may sound unreliable to law enforcement personnel and to the general public and may therefore never make it to court. One striking example of this is that an estimated 86% of sexual assaults are never prosecuted on the grounds that the victim's testimony does not seem to be reliable[31].

How memory distortions occur

Memory distortions can occur in different ways. Many distortions involve some form of explicit or covert misleading information. One form of this phenomenon, the misinformation effect, has been thoroughly studied for the past 30 years[4]. This effect refers to a distortion of an original memory after being exposed to misleading information related to that memory: for example, an impairment in the memory of the face of a perpetrator after being exposed to a photo of a police suspect who was not the true perpetrator. This 'misinformation' is considered misleading in that it detracts from the original memory, not because it is purposefully deceitful. Laboratory studies have shown that it is possible to induce memories in a participant that are entirely false, such as a special hospital visit at the age of 4 years when no such visit happened[4]. Misleading information is often given unintentionally and can be as subtle as slight variations in the wording of a question. For example, when participants viewed footage of a car accident, the question 'how fast were the cars going when they smashed into each other?' elicited reports of 20% greater travelling speeds than the question 'how fast were the cars going when they hit each other?', despite the fact that participants in both conditions viewed the same footage[2]. The question with the word 'smashed' was also more likely to elicit a false memory of broken glass at the site of the crash[2]. Witnesses are often called to testify on specific details such as these, and their reports may influence the likelihood of conviction and the degree of punishment — for example, a harsher crime sentence for travelling at higher speeds.

Distortions in memory can also occur from feedback provided to the witness after their testimony. Positive post-identification feedback, such as informing a witness that their choice in a suspect line-up matched the police suspect or was the same as that of other witnesses, increases the eyewitness's level of confidence in their choice[32,33]. Positive post-identification feedback also increases a witness's later estimate of the amount of attention that he or she paid to the crime and of how well they could see the scene and/or perpetrator[33,34]. Conversely, negative feedback can deflate confidence in a memory and other measures[32,35]. In addition, non-verbal feedback via body language and facial expressions can occur if the officers conducting the line-up are aware of which individual is the police suspect[36]. Even in the absence of feedback, mere repeated questioning about an event can increase a witness's confidence in the accuracy of their memory[37]. Such changes in a witness's reported estimations of confidence and attention are highly relevant in the courtroom, as judges and jurors often use these factors as indications of the accuracy and reliability of a witness's testimony.

Memory distortions can even occur in highly trained individuals. One series of studies examined highly trained, specifically selected military personnel in survival school who received a week of classroom instruction on how to handle stressful interrogations before they were exposed to a mock prisoner of war camp (POWC; see BOX 3)[38,39]. The mock POWC provides a controlled setting, which simulates realistic and personally relevant stress. In one study of over 500 active-duty military personnel, participants were asked to identify their interrogator after being released from the mock POWC. These individuals had had a clear view of their assailant during the 30–40-minute interrogation. However, only approximately one-third of the identifications were correct. Strikingly, the subjects identified someone in the line-up as the interrogator in almost two-thirds of cases in which the actual interrogator was not present in the line-up[38]. A related study involving a population of over 800 military personnel revealed that interrogator identifications were also easily influenced by misinformation. For example, exposure to a misleading photograph (that is, a photograph of someone who was not the interrogator) before identification increased the likelihood of a false identification[39]. The misidentifications that occurred with and without exposure to misinformation were robust, despite the fact that these studies involved a select group of individuals thought to be superior in their ability to handle stressful situations. Although a limitation of these studies is that subject selection may be biased because they involved participants who chose to enrol in survival school, their findings converge with data from laboratory-based studies of eyewitness testimony under highly stressful situations[40,41] and the misinformation effect[4].

Memory distortions can also occur simply with the passage of time and with repeated recounting of events. Although it might not be surprising that mundane memories become weaker and more susceptible to distortion over time, emotional and traumatic 'flashbulb memories' are also susceptible to these automatic distortions. For example, after the terrorist attacks of 11 September 2001 on New York City, US citizens were asked to remember when they first heard about the attacks. They were asked to recall this episode approximately 1–2 weeks after the attacks, 1 year later and 3 years later[6]. Memories of the details had changed in 37% of the people after 1 year and in 43% after 3 years. Interestingly, despite the drop in memory accuracy, confidence in the accuracy of the memory remained high — an example of a negative relationship between memory confidence and accuracy — and was driven primarily by attention paid to media reports and by talking about the attack in the intervening time[6].

Box 2 | **The Innocence Project**

In 1981, Linda Mae Craig, a young sales associate, was abducted from her car on her way home from work. The next day, her body was found in a church parking lot, beaten and sexually assaulted. Days later, 20-year-old Nicholas Yarris was stopped for a routine traffic violation, which escalated into a physical altercation and resulted in Yarris being taken into custody. In a bid to speed his release from custody, Yarris told police that he believed an acquaintance was involved in the murder. However, when the acquaintance's alibi was cleared, Yarris became the chief suspect. After a short trial, which involved eyewitness testimony from the victim's co-workers, Yarris was sentenced to death row and solitary confinement for the kidnapping, rape and murder of Craig. Yarris spent over 21 years behind bars before he was exonerated through DNA testing. He was the thirteenth individual in the United States to be exonerated from death row.

Yarris's story is one of hundreds recorded by the Innocence Project, a non-profit ligation organization in the United States. According to their data, exonerees spend an average of 13.6 years in prison before being released. After exoneration, there is little support or assistance. The average compensation, which is not guaranteed, amounts to US$24,000 per year for each year spent behind bars, often capping at a maximum of 10 years. This does not take into consideration the money exonerees have spent on legal fees. Not only have they lost precious and prime years of their life, many exonerees are never acknowledged as victims of legal injustice. They find it difficult to regain a normal life after release from prison. Many have lost friends and family over the years in confinement and bear the social stigma of being regarded as a criminal, which leads to difficulties in finding employment, even after their record is cleared.

Eyewitness testimony plays a part in roughly 75% of all cases in which individuals are wrongfully convicted[24]. The Innocence Project aims to reform the criminal justice system by raising awareness of these issues and advocating changes in public policy.

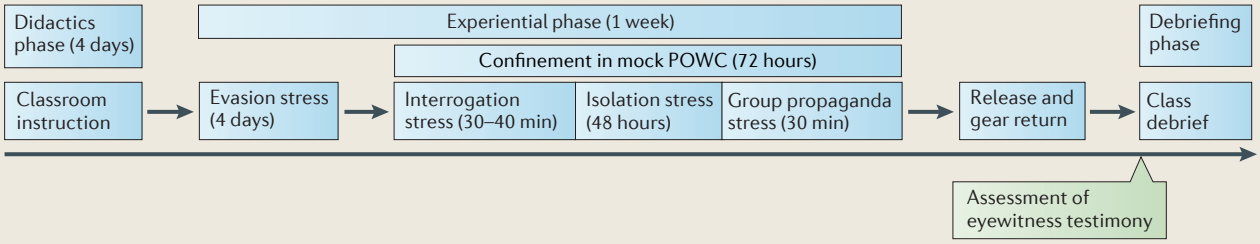
Box 3 | **Mock-'prisoner of war camp' studies on eyewitness identification**

Although eyewitness testimony has been empirically studied for decades, most research involved videotaped scenes or live simulations of crimes. A critique of such laboratory experiments is that they lack personally relevant and realistic stress. A few studies did involve actual crimes[27,89,90], but these studies suffered from a lack of control over the amount and duration of stress as well as objective data on the true perpetrator. The mock-'prisoner of war camp' (POWC) portion of military survival school, which enlists only the most highly trained military personnel, provides an ideal venue to study eyewitness identification in a highly realistic but controlled setting. High levels of personally relevant stress can be applied in a uniform and consistent manner to all participants. The levels of stress induced in mock-POWC participants have noticeable physiological and psychological effects[91] that are on par with real-world threats such as combat.

Survival school begins with a week of training to prepare students for the mock POWC, including training to withstand intense interrogation and to resist counter-cultural propaganda. During the mock POWC, each participant is placed in isolation, deprived of food and uniform sleep for approximately 48 hours and is interrogated in a manner that threatens physical violence (for example, slapping, punching and submission positions[39]). Interrogations last 30–40 minutes, and participants have a clear view of their interrogator the entire time. The participants are asked to identify their interrogator approximately 24 hours after being released from the mock POWC and after being given access to food and sleep (see the figure). In some cases, they were given misinformation before making identifications.

One mock-POWC study with over 500 survival camp attendees implemented three different types of line-up[38]: live, in-person line-ups; simultaneous photo line-ups, in which photos of possible interrogators are shown at the same time, and witnesses must select the interrogator (if present) in the photo spread; and sequential photo line-ups, in which photos of possible interrogators are shown one at a time, and witnesses must decide for each of them whether they were the perpetrator. Participants correctly identified their interrogator in ~33% of cases in which the interrogator was present in the line-up. When the interrogator was not present in the line-up, participants made false-positive identifications (that is, they identified an 'innocent' person as the interrogator) in almost 66% of cases. These mock-POWC results support previous findings that sequential line-ups elicit fewer misidentifications than do simultaneous line-ups[84]. Another POWC study involving a separate population of over 800 military personnel[39] has replicated findings of the misinformation effect[4]: exposure to misleading photographs or leading questions increased the likelihood of false identifications or inaccurate memories.

The participants of survival school are successful military personnel who are often selected for their perceived ability to handle high-stress situations. Strikingly, these mock-POWC studies show that even such highly trained individuals are susceptible to memory distortions and making false identifications, and are influenced by misinformation. Figure is modified, with permission, from REF. 39 © (2013) Elsevier.



These types of memory distortion increase as we age. For example, false memory for words that were not in a list of words presented to the participant but that were semantically related to the words on the list (a test known as the Deese–Roediger–McDermott paradigm) increases with age[3]. Similarly, when shown lists of objects, some of which are similar but not identical to previously seen objects, older participants are more likely than younger participants to incorrectly identify these as being repeated objects[42]. By contrast, correct identifications of repeated items and of novel items unrelated to the listed items are largely unaffected by age. Thus, ageing seems to be associated with an over-generalization of memories, such that an event that is similar to a prior event is more often remembered as being identical to the prior event. Aged individuals are also more susceptible to the misinformation effect than are young adults[4,5]. Thus, as people age, memory for the gist of an event may remain intact, but memory for specific details of the event degrades, and individuals are more likely to falsely incorporate similar information into their memories.

The fallibility of memory has implications for the question of how much weight should be given to eyewitness testimony in court cases. In addition, jurors are subject to memory biases. For example, when mock jurors listened to audio recordings of a mock trial, they 'recalled' 15% of details of that were not mentioned in the trial but that fit a typical crime description (for example, 'pulled out a gun' was never stated but fits the description of a robbery)[43]. This reflects people's natural bias to 'fill in the gaps' of a memory, but such fill-ins are inaccurate accounts of the actual events. The occurrence of false memories can be increased by leading questions, such as those that might be asked by prosecutors. Mock jurors 'recalled' 25.8% of details that were implied in leading questions from the prosecuting attorney in a mock trial but that were not stated by the eyewitness of the trial, suggesting that jurors have difficulty in sorting statements from eyewitnesses and attorneys. Moreover, even when mock jurors were given explicit instructions to focus on the testimony of witnesses and not on information implied from attorneys, they still 'recalled' 20.4% of details that were not mentioned in the eyewitness testimony[43]. Thus, such instructions to jurors only marginally reduced the effect of leading questions and did not completely prevent it.

Insights from the neuroscience of memory

Our understanding of the neurobiological mechanisms of memory formation, consolidation and retrieval can explain, at least to some extent, why some types of memory distortions occur and why imperfect memory is the norm. At the cellular and molecular levels, these mechanisms are thought to involve processes linked to long-term potentiation (LTP) and long-term depression (LTD).

LTP and LTD. Hebb[44] proposed a conceptual framework that linked associative memory formation to activity-dependent changes in the strength of connections in a network, and Bliss and Lømo[45] provided the first direct evidence for such a link. They found that by strongly stimulating the perforant pathway from the entorhinal cortex to the

Glossary

Lie detection training
Classroom instruction given to law enforcement personnel on how to detect subtle cues of deception.

Misinformation effect
A distortion in an original memory or the creation of a false memory after being exposed to misleading information related to the memory. The 'misinformation' is considered 'misleading' as it detracts from the true memory, not because it is purposefully deceitful.

War of the Ghosts
A Native American fable. It was used by Barlett to show that it was difficult for English participants to recall the fable precisely because it did not fit into their conceptual framework; that is, English participants were not familiar with Native American traditions, and they therefore tended to reinterpret the story in a context more in line with English culture.

Weapon focus
The tendency for a witness's attention to be drawn to a weapon, thereby increasing subsequent memory for the weapon but impairing memory for the perpetrator.

dentate gyrus, they had increased the ease with which neurons in the entorhinal cortex could excite neurons in the dentate gyrus. This strengthening of the connections remained quite stable and was dubbed LTP. LTP is activity-dependent and requires coincident firing of pairs of neurons. Thus, the learning rule underlying LTP corresponds quite well to the associative learning rule posited by Hebb. There is now substantial evidence that LTP, or at least a similar process that shares many mechanisms with LTP, underlies numerous forms of learning and memory[46].

A great deal has been learnt about LTP, its mechanisms, and its various forms. For example, depolarization without activation of NMDA receptors and protein synthesis results in an 'early' Hebbian form of LTP that only lasts for several hours. By contrast, NMDA receptor-dependent LTP leads to structural changes that show little sign of degradation with time[47]. This could suggest that once a memory undergoes such 'synaptic consolidation' and is associated with the structural changes of late-phase LTP, it is immutable. Unfortunately, this is not the case; as these changes are not permanent, nor are the memories that have been thus encoded indelible. Although coincident firing of neurons can lead to LTP and the strengthening of a memory, if the neurons fire in an uncorrelated way (as may be the case if the neurons individually activate in different experiences and therefore in different memories) this leads to the opposite effect — namely, a reduction in the strength of the same synapses that were strengthened by LTP. Thus, there is a mechanism, known as LTD, for weakening synaptic connections — and therefore presumably memories — as well. Importantly, LTP and LTD occur at the level of individual synapses, and the same individual neurons and synapses are probably involved in several or many memories[48], leading to the potential for interference of one memory with another[49] and suggesting that the learning of new information can overwrite previously learned information by changing the strengths of the synapses that had been used to encode that information. Conversely, as noted above, previously learned information (experiences, biases, and so on) can influence the learning of new information.

Moreover, there is evidence at the molecular level that memories can be lost or altered. First, the maintenance of LTP appears to be an active process, as administering zeta-inhibitory peptide can depotentiate synapses and erase memories[50,51]. Second, the act of retrieving a memory (that is, reactivating a memory) is thought to put that memory and the potentiated synapses associated with the memory into a labile state, from which it must restabilize in order to persist. Without this process, known as 'reconsolidation' (which, like long-lasting LTP, requires protein synthesis), the information is lost[52]. This reconsolidation process is thought to be functionally beneficial, as it provides the system with an opportunity to strengthen or weaken a memory or to update its contents[53]. If the content of a memory is updated at the time of retrieval, memory distortion could occur, of which the individual would presumably be entirely unaware[53].

Note that thus far, we have discussed how the contents of an existing memory may be changed. There is also reason to believe that more recent memories can compete with older memories at the time of retrieval, leading to memory errors when trying to retrieve the original information[54]. That is, if two different memories of an event exist (for example, the original memory and a memory formed while retelling the event) or if there are two overlapping memories (for example, the original memory of the event in question and memories of a subsequent event that shares several of the same components), attempting to retrieve the original event may inadvertently and unknowingly draw upon information from the second event. There are neurobiological findings that support this mechanism for altering memory performance. For example, the extinction of a conditioned response engages many (although perhaps not all) of the same mechanisms that were engaged during the initial learning of the response[55], supporting the notion that extinction is not simply the loss of an existing association but involves new learning. The phenomena of spontaneous recovery (reappearance of a previously extinguished memory) and disinhibition (re-emergence of a conditioned response after experiencing a novel stimulus) also support this notion.

Generalization over time and with retrieval. Memory distortions in humans may occur simply with the passage of time. This is partly because over time, memories typically become less episodic (highly detailed and specific) and more semantic (more broad and generalized), as the information is repeatedly retrieved and re-encoded in varying contexts. This generalization of a memory over time has also been observed in animals. For example, if a rodent receives an electric footshock in a particular context, subsequent exposures to that context induce a 'freezing' behaviour[56]. The specificity of the memory can be probed by exposing the animal to a different context. Comparing the levels of freezing in the two contexts reveals how well the animal discriminates between them (FIG. 1). A typical finding is that freezing in the training environment may not degrade much with delay (that is, the animal shows little forgetting of the memory) and that the level of freezing in the other context is initially very low. However, freezing in the other context typically increases with delay, indicating a reduction in the ability to discriminate between the contexts in memory or an increased reliance on the 'gist' of a context than on specific contextual details[57,58]. Thus, even highly salient, strong memories, such as the memory of receiving a shock, that are initially detailed and specific become more generalized with the passage of time. Such generalization is stronger for similar contexts than for highly dissimilar ones, and the hippocampus is required to differentiate between contexts, as it maintains the representations of the details that distinguish them[59]. Interestingly, a recent study in mice suggests that it may be possible to experimentally induce a false fear memory by stimulating the hippocampal neuronal representation of context A while the rodent is being shocked in context B[60].

During the formation of a new episodic memory, information about a related memory can be automatically retrieved.

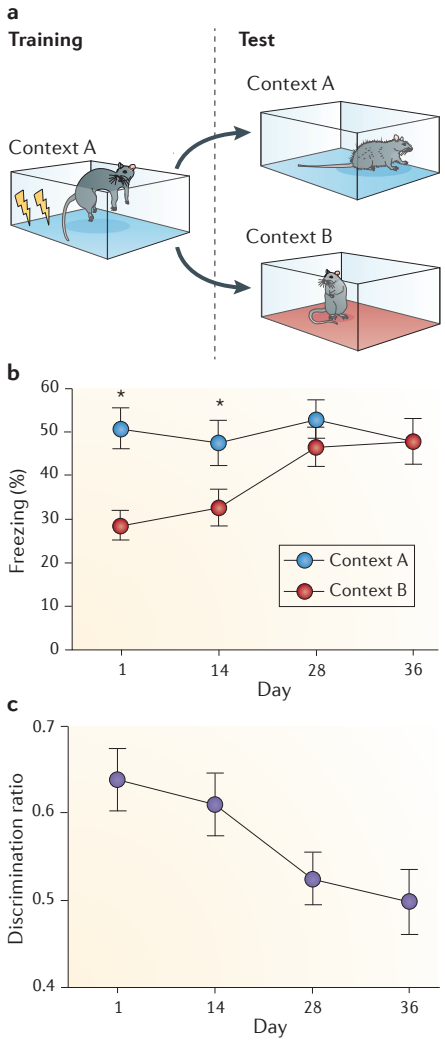


Figure 1 | **Memory generalization over time in rodents.** **a** | Rats were exposed to a training context (context A) and given a small shock in that context, which induces 'freezing' behaviour (a common fear response in rodents). After a delay, they were placed in either the training context (context A) or a novel context (context B). Memory for the shock and the specific environment in which it was given was assessed by measuring the amount of time the rats spent freezing in each context. **b** | One day after training, rats froze less in the novel context than they did when re-exposed to the training context. This behaviour indicates memory of the specific context in which they were shocked. **c** | This ability to discriminate between the two contexts (that is, the discrimination ratio) decreases with time: rats that were tested 4 weeks after training froze an equal amount of time in the training context and the novel context. This suggests that at this time, both the training and test contexts (both of which involve the rat being removed from the home cage, taken to another room and placed in a box) match the contents of the memory. Parts **b** and **c** are modified, with permission, from REF. 57 © (2007) Cold Spring Harbor Press.

New learning taking place to encode this new episode can 'spill over' and alter the contents of this automatically retrieved information. For example, in one study[61], rats were exposed to two distinct contexts (A and B) every day for several days, so that some association would probably be formed between the two contexts (A–B). The rats were then exposed to one of the contexts (B). Given the prior training, rats probably retrieved a memory of the other context (A), and at this point, rats were given a shock. Subsequently, the level of freezing the animals showed in context A was higher than that in a novel context (C)[61]. This finding is consistent with the idea that being placed in the B context reactivated the memory of context A, so that the association between context B and shock 'spilled over' to form a false association between context A and shock. Just like the learning of accurate associations, the learning of this inaccurate retrieval-mediated association relies on NMDA receptors in the hippocampus[62].

Thus, experiencing an event can lead to the automatic retrieval of information that is not present but has previously been associated with similar events. Given that a goal of our memory system should be the use of prior information to guide current behaviour in an adaptive manner, such automatic retrieval of memories from related events would be expected. The problem is that learning is occurring at this point and that it does not clearly discriminate between the current event and retrieved information from specific prior events or from generalized expectations of what should happen in such an event. As a result, whatever happens in this event becomes associated not just with elements that are actually present but also with what we expect to be present based on our prior experiences and biases. This phenomenon was shown in an elegant functional MRI (fMRI) study in humans[63]. Here, participants initially encoded a series of image pairs (A–B) while undergoing fMRI. After testing the memory for these pairs, they again encoded a series of image pairs during fMRI. Some of these pairs repeated an element from the initial encoding list (A–C). During this second encoding phase, activity of the hippocampus provided evidence for the reactivation of previous, related events (A–B). The amount of hippocampal activity for the original A–B event during this related A–C retrieval predicted how much of the original A–B information was lost and how much of the novel A–C information was retained[63].

It is important to note that even without considering the notion of deception, it is difficult to distinguish true memories from false memories by examining brain activity. The relative amount of hippocampal activity during the encoding of an event and during subsequent encoding of misinformation predicts which version will be remembered, even when participants are confident in the accuracy of their false memory[64]. Thus, the formation of true and false memories appears to involve the same processes. At the time of retrieval, differences in activity in early sensory regions for true versus false memories can be observed[65,66], which is consistent with findings that true memories contain greater sensory detail than false memories[3,67]. Some regions in the prefrontal cortex may be more active during the formation and/or retrieval of false memories than they are during the formation and/or retrieval of true memories[68]. However, these differences in activation cannot discriminate true from false on a trial-by-trial basis[68]. These differences may also fade over time. This is important in the context of eyewitness testimony, as the time elapsed between witnessing an event and testifying about it in court may render brain activity measures useless for distinguishing true from false memories. Last, most differences in brain activity are observed in early sensory regions of the cortex, which are not typically associated with conscious awareness, suggesting that we may not be able to consciously know the truth even if some regions of our brains could differentiate true from false memories.

The closest that experimenters have come in being able to distinguish true from false memories on a trial-by-trial basis is with the use of multivoxel pattern analysis (MVPA), a relatively novel method of analysing fMRI data using pattern classifiers that learn to use stimulus-related activity across voxels to categorize stimuli. MVPA can distinguish subjectively remembered images (that is, images for which the person has the mnemonic perception that he or she has seen them before) from forgotten images with ~70–75% accuracy[69]. However, MVPA classifiers performed either at chance or only marginally above chance when trying to distinguish between objectively true and false memories — far below their accuracy for subjective memory[69]. Thus, even the most cutting-edge neuroimaging techniques are currently unable to distinguish between objectively true and false memories by analysing brain activity.

Stress and memory. It is well established that arousal and the stress hormones adrenaline and cortisol that are released during arousal can modulate synaptic consolidation and memory strength[70]. Decades of research have supported the view that emotional arousal leads to activation of the basolateral amygdala (BLA), which modulates memory storage, leading to more strongly encoded memories[70]. This does not imply, however, that memories encoded during a state of heightened arousal cannot be lost or distorted. In fact, high levels of stress during an event are not necessarily associated with an increase in memory strength for that event and can even result in a reduced memory for the event. Indeed, in both animals and humans, there is an inverted U-shaped dose–response relationship between plasma stress hormone levels and memory performance[70,71]. Very high levels of stress during an event are not necessarily associated with an increase in memory strength for that event and can even result in a reduced memory for the event. For example, high levels of either endogenous or exogenous cortisol in humans can impair declarative memory formation[72]. Thus, in states of high arousal, such as witnessing a crime or being a victim of crime, memory encoding may be enhanced or impaired depending on the person's individual stress response.

Emotional arousal during an event has effects during retrieval of the memory of that event as well. The retrieval of arousing information leads to a reactivation of the BLA, which can lead to further strengthening of memory[73]. However, distortions can occur if any aspect of the retrieval or reconstruction of the memory is erroneous: as the retrieved information is re-encoded, these distortions (whether they are self-generated or externally suggested) can potentially become part of the memory. In addition, in humans, high levels of the stress hormone cortisol during retrieval (either administered exogenously[74] or induced endogenously[75]) have been shown to impair the retrieval of personal autobiographical memory. Importantly, arousal may enhance memory for some aspects of an event and impair memory for other aspects. For example, violence and trauma tend to improve memory for the central gist of an event (for example, witnessing a homicide) but impair memory of the peripheral details of the event (for example, the clothing of the perpetrator)[40,41].

Clearly, the relationship between stress and memory is complicated. Veridical memories may not always be accompanied by a high level of confidence and details. In particular, victims of violent or otherwise upsetting crimes may have vague and disjointed memories of the event, especially during a first interview soon after the crime, when stress levels are still high. It should not be surprising if a second interview, conducted when the stress hormones have returned closer to baseline levels, contains a more coherent story, with additional details that were not recalled on the first interview. Even without stress, memory retrieval is a probabilistic process. This was first shown by Ebbinghaus[1] for retrieval of simple, neutral lists of syllables. As stress is added into the process, the picture is clouded even more. The data discussed above suggest that the stress of witnessing a crime or the stress of the first interview can either enhance or impair the encoding and retrieval of the crime event. Stress will therefore also affect the likelihood of establishing false memories during a second interview. Laboratory studies have shown that over time, false memories are more likely to be endorsed as real memories, and these false memories tend to include more peripheral details with time[76–78]. Thus, there is no set rule that information retrieved across multiple interviews is inherently true or false. A broader understanding of memory processes (including the effects of emotion and time), situational factors (how stressful was the experience to the witness), and testimony consistency (what information was consistent or incongruent across interviews) must be taken into account when considering information provided by eyewitnesses.

Application to courts

The data reviewed above show that memory is imperfect and that we cannot assume that this is well understood by the general public and by the courts. Relatively simple changes in procedures can help to reduce the occurrence of memory distortions. Even in situations in which the possibility of memory distortions cannot be avoided, judges and jurors can be better educated on the limitations of memory. The fact that memory is imperfect cannot be changed, but perhaps we can change how much weight is placed on evidence drawn from memory and on the confidence ascribed to memory.

Most of the time, peripheral details of events are of low importance and are therefore often not well recalled. However, in the courtroom, witnesses are often called to testify on precisely such very specific details. Some witnesses may give accounts that are missing details, that are hazy in places and that may even have some amount of demonstrable distortion. They may report that they are unconfident about much of the memory as well. Other witnesses with the same actual amount of information available for retrieval may present far clearer, more detailed accounts, with strong confidence in the accuracy of their memory. In these witnesses, the extra information presented and the confidence in the recall would be driven by the reconstructive nature of memory retrieval, as described above. Thus, although in general, accurate memories are more confidently recalled and more detailed than inaccurate memories, jurors should be aware that sometimes vague, somewhat distorted memories may be more veridical than very detailed and confident accounts. Given what we know about the neurobiology of memory and the cognitive psychological research on memory, 'perfect' memories that are accompanied by a high level of confidence and detail should be taken with a grain of salt, and 'imperfect' memories that are vague and missing details should not be immediately discredited. However 'good' a witness's memory of an event may be, their memory may not actually be accurate, and currently there is no clear way to measure the accuracy. This does not mean that memory-based evidence should be disregarded but rather that police, judges and jurors should be educated on these nuances so that they may give memory-based evidence its proper weight.

Interviewing eyewitnesses. Although the relationship between confidence in the accuracy of a memory and the actual accuracy of a memory is complex, confidence statements should be recorded immediately after an interview or suspect identification[24], before the witness's subjective feeling of confidence can be influenced by post-identification feedback[32–35] or other factors[36,37]. If confidence is to be used as an indicator of memory accuracy, this would be the best estimate of confidence to use.

There is a large literature on different approaches to interviewing eyewitnesses. The cognitive interview, sometimes referred to as the 'enhanced' cognitive interview, was developed by psychologists in response to a request from law enforcement for better interviewing methods[24,79]. Here, we will review the general outline of the cognitive interview, as it lays a solid foundation for best practices.

Interviewing should begin with a transfer of control to the witness; that is, witnesses should be put at ease and made to feel comfortable. This is important in avoiding unintentional bias, as witnesses may

be easily manipulated by individuals with perceived power and authority, such as law enforcement personnel. It is recommended that officers ask the witness to mentally recreate the scene of the crime. This is based on research on context-dependent memory, which has shown that recall is better when it occurs in the same context as learning[80].

Testimony ought to begin with an open-ended narrative; that is, witnesses should be encouraged to recall as much detail as possible, even if they recall events out of order or the details seem trivial. The interviewer should allow time for long pauses while the eyewitness thinks, relaxes and gathers his or her thoughts. This approach contrasts with standard police interviews, in which a witness may often be interrupted and asked to report events in a specific order. Allowing witnesses to report events in their own order and at their own pace results in a more detailed and more accurate report[24]. Witnesses should be asked to indicate when they are unsure and should be informed that they should not guess.

After the free narrative, the interviewer can follow up with open-ended questions, keeping in mind that the wording of a question can lead to memory distortions (as discussed above). Indefinite articles should be used over definite articles. For example, asking whether the witness saw 'the gun' as opposed to 'a gun' implies that a gun was present[2]. Last, it should be kept in mind that congruency among multiple eyewitness accounts does not necessarily entail greater accuracy, as witnesses may communicate with each other and all are susceptible to the same memory errors.

Identification of suspects. There are many guidelines for constructing and conducting suspect line-ups. These guidelines suggest that each line-up should only contain one suspect and that the suspect should not stand out from the rest of the line-up. Fillers (other non-suspects in the line-up) should be selected on the basis of the eyewitness's description of the perpetrator. If an innocent suspect fits the description of the perpetrator more than the other people in the line-up, there is a higher likelihood that the suspect will be misidentified as the perpetrator. In a truly unbiased line-up, naive 'mock witnesses' who did not witness the crime should not select any one individual more frequently than the others[2,24].

Although no line-up method can completely eliminate false identifications and increase the likelihood of a correct identification, some recommendations will reduce the number of misidentifications without substantially reducing the likelihood of a correct identification. The first is to warn witnesses that the true perpetrator may not be present in the line-up. Research has found that experimental witnesses have a tendency to select a suspect even if the actual target is not in the line-up[38,39]. The instruction that the suspect may not be present in the line-up has substantially reduced the number of misidentifications, especially in line-ups in which the target was absent. Although the number of correct identifications was also reduced in these studies, this was only to a small degree[24,81]. Second, sequential line-ups (in which the potential suspects are shown one after the other) tend to produce fewer false identifications than simultaneous line-ups (in which all potential suspects are shown together) (BOX 3). This approach also reduces the number of correct identifications but typically only to a small degree[82,83]. The adoption of these procedures has met resistance, which is generally based on the fear that it may lead to fewer convictions of guilty suspects[84]. Although these procedures may indeed increase the number of type I errors (no identification of guilty suspects and therefore fewer convictions), they reduce the number of type II errors (wrongful identification of innocent suspects and therefore wrongful convictions) without a cost to overall accuracy; that is, they lead to a shift towards more conservative identification, which favours protecting innocent suspects.

As previously discussed, distortions in memory can occur as a result of post-identification feedback, whether intentional or not[32–35]. Double-blind line-ups, in which the official who administers the line-up does not know who the police suspect is, would reduce such unintentional bias[24]. One critique against using double-blind line-ups has been the cost of and need for extra manpower to administer these line-ups. However, computer programs can be used to administer the line-ups in a blind fashion by showing photos of suspects on a computer screen without any police officers being present, thereby alleviating this concern.

Recommendations for judges and jurors. It is important to remember that the courtroom also places large demands on the memory of judges and jurors. Jurors are often faced with complex legal instructions and procedures. Simple, clearly written instructions from judges help to clarify the deliberation process. In particular, given the data described above concerning misinformation[2,4], jurors should be warned of the effects of misleading questions by attorneys. Jurors are subjected to prosecutors and defence attorneys who may deliberately try to confuse them, redirect their attention and play to their emotions. There are opportunities for retroactive and proactive interference, as lawyers interject arguments during the court proceedings. In particular, misleading questions may imply that facts were presented in evidence by a witness that were not actually presented. Although such education does not eliminate the tendency to incorporate information based on biases, it does reduce its effects[43].

Jurors should likewise be instructed that the memory of an eyewitness should not be considered indelible, even if the event was traumatic[38–41]; that a person's biases and expectations will change with time and new information (or misinformation[4,39]), and that this can alter the memory; that a witness's confidence that their memory is accurate is no guarantee that the memory is indeed accurate[6,27,30,33–35]; and that even what is encoded in the first place is filtered by a person's preconceived notions and schemas[85], and that people have a tendency to 'fill in the gaps' in a memory[43]. An understanding of these issues may help jurors to realize that eyewitness testimony is not equivalent to DNA evidence in terms of probative value. Some regional jurisdictions the United States, such as New Jersey[9,10], Massachusetts[11], Texas[12] and North Carolina[13], have begun to provide instructions to jurors on how to approach eyewitness testimony[9,11–13].

In addition, it is recommended that jurors be allowed to take notes, as the sheer amount of information presented to jurors often exceeds reasonable demands on memory capacity. As jurors are eyewitnesses to the events in the courtroom, their memories of these events may also be vague and may be reconstructed based on biases, prior beliefs and expectations, and misinformation. Courtroom transcripts may be available, but they are often not useful because jurors have difficulty finding the pertinent information in the lengthy transcripts. Taking notes not only provides a source of reference but improves the memory itself[86]. Although some might argue that a juror who takes notes might dominate deliberations, encouraging all jurors to take notes could overcome this problem. Like eyewitnesses, a juror espousing great confidence in his or her recollection is more likely to be trusted. It would be beneficial to at least have this trust based on notes rather than on memory alone.

Conclusions

Memory is imperfect and susceptible to distortion and loss. There are adaptive reasons for generalization and forgetting[7]. Indeed, Luria's famous report of the mnemonist S.[87] readily shows how an inability to forget can severely impair normal functioning. In addition, the neurobiological mechanisms that underlie the occurrence of distortions in memory also allow memories to be updated and strengthened. Unfortunately, in the courtroom, 'memory' is often misunderstood and undue assumptions are made about its veridicality.

Thus, there needs to be greater education and awareness of memory processes in judicial settings and in daily life. Society would benefit from a better understanding of what factors affect the accuracy of memory and of their complexity and potentially counterintuitive nature. Second, the legal system needs to re-evaluate the probative value of memory. Witnessing a potentially traumatic event does not produce an unbiased, indelible memory of the event. Memory is an adaptive process based on reconstruction. It works well for what it is intended — guiding current and future behaviour. However, it is not infallible and therefore should not be treated as such. For these reasons, some have argued that the legal system should not convict individuals based on eyewitness testimony alone but rather should require corroborative evidence[84,88]. Last, more research ought to be carried out on the complex mechanisms that underlie memory so that we can better understand its limits, improve its reliability and detect when it has gone awry.

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1. Ebbinghaus, H. *Memory: a Contribution to Experimental Psychology* (Teachers College, Columbia Univ., 1885).
2. Loftus, E. F. *Eyewitness Testimony* (Harvard Univ. Press, 1979).
3. Norman, K. A. & Schacter, D. L. False recognition in young and older adults: exploring the characteristics of illusory memories. *Mem. Cogn.* **25**, 838–848 (1997).
4. Loftus, E. F. Planting misinformation in the human mind: a 30-year investigation of the malleability of memory. *Learn. Mem.* **12**, 361–366 (2005).
5. Dodson, C. S. & Krueger, L. E. I misremember it well: why older adults are unreliable eyewitnesses. *Psychon. Bull. Rev.* **13**, 770–775 (2006).
6. Hirst, W. *et al.* Long-term memory for the terrorist attack of September 11: flashbulb memories, event memories, and the factors that influence their retention. *J. Exp. Psychol. Gen.* **138**, 161–176 (2009).
7. Schacter, D. L., Guerin, S. A. & St Jacques, P. L. Memory distortion: an adaptive perspective. *Trends Cogn. Sci.* **15**, 467–474 (2011).
8. Simons, D. J. & Chabris, C. F. What people believe about how memory works: a representative survey of the U. S. population. *PLoS ONE* **6**, e22757 (2011).
9. State v. Henderson, 208 N.J. 208 (2011).
10. Schacter, D. L. & Loftus, E. F. Memory and law: what can cognitive neuroscience contribute? *Nature Neurosci.* **16**, 119–123 (2013).
11. Massachusetts Commonwealth v. Silva-Santiago, 906 N.E.2d 299 (2009).
12. Texas State Government. Art. 38.20. Photograph and live lineup identification procedures. *Texas Constitution and Statutes* [online], http://www.statutes.legis.state.tx.us/Docs/CR/htm/CR.38.htm (2011).
13. North Carolina State Government. Article 14A. Eyewitness Identification Reform Act. 15A-284.50 *North Carolina General Assembly* [online], http://www.ncga.state.nc.us/EnactedLegislation/Statutes/HTML/ByArticle/Chapter_15A/Article_14A.html (2007).
14. Deffenbacher, K. A. & Loftus, E. F. Do jurors share a common understanding concerning eyewitness behavior? *Law Hum. Behav.* **6**, 15–30 (1982).
15. Kassin, S. M., Ellsworth, P. C. & Smith, V. L. On the "general acceptance" of eyewitness testimony research: a survey of the experts. *Am. Psychol.* **44**, 1089–1098 (1989).
16. Benton, T. R., Ross, D. F., Bradshaw, E., Thomas, W. N. & Bradshaw, G. S. Eyewitness memory is still not common sense: comparing jurors, judges and law enforcement to eyewitness experts. *Appl. Cogn. Psychol.* **20**, 115–129 (2006).
17. Read, J. D. & Desmarais, S. L. Lay knowledge of eyewitness issues: a Canadian evaluation. *Appl. Cogn. Psychol.* **23**, 301–326 (2009).
18. Kassin, S. M., Tubb, V. A., Hosch, H. M. & Memon, A. On the "general acceptance" of eyewitness testimony research: a new survey of the experts. *Am. Psychol.* **56**, 405–416 (2001).
19. Meissner, C. A. & Brigham, J. C. Thirty years of investigating the own-race bias in memory for faces: a meta-analytic review. *Psychol. Public Policy Law* **7**, 3 (2001).
20. Schacter, D. L. *The Seven Sins of Memory: How the Mind Forgets and Remembers* (Houghton Mifflin Company, 2001).
21. Bartlett, F. C. *Remembering: a Study in Experimental and Social Psychology* (Cambridge. Univ. Press, 1932).
22. Neisser, U. *Cognitive Psychology* (Appleton-Century-Crofts, 1967).
23. Sulin, R. A. & Dooling, D. J. Intrusion of a thematic idea in retention of prose. *J. Exp. Psychol.* **103**, 255–262 (1974).
24. Wells, G. L., Memon, A. & Penrod, S. D. Eyewitness evidence: improving its probative value. *Psychol. Sci. Public Interest* **7**, 45–75 (2006).
25. Dunlosky, J. & Metcalfe, J. *Metacognition* (Sage Publications, 2009).
26. Wixted, J. T. & Mickes, L. A continuous dual-process model of remember/know judgments. *Psychol. Rev.* **117**, 1025–1054 (2010).
27. Odinot, G., Wolters, G. & van Koppen, P. J. Eyewitness memory of a supermarket robbery: a case study of accuracy and confidence after 3 months. *Law Hum. Behav.* **33**, 506–514 (2009).
28. Kassin, S. M. & Fong, C. T. "I'm innocent!": effects of training on judgments of truth and deception in the interrogation room. *Law Hum. Behav.* **23**, 499–516 (1999).
29. Meissner, C. A. & Kassin, S. M. "He's guilty!": investigator bias in judgments of truth and deception. *Law Hum. Behav.* **26**, 469–480 (2002).
30. Kassin, S. M., Meissner, C. A. & Norwick, R. J. "I'd know a false confession if I saw one": a comparative study of college students and police investigators. *Law Hum. Behav.* **29**, 211–227 (2005).
31. Campbell, R., Patterson, D. & Bybee, D. Prosecution of adult sexual assault cases: a longitudinal analysis of the impact of a sexual assault nurse examiner program. *Violence Against Women* **18**, 223–244 (2012).
32. Semmler, C., Brewer, N. & Wells, G. L. Effects of postidentification feedback on eyewitness identification and nonidentification confidence. *J. Appl. Psychol.* **89**, 334–345 (2004).
33. Wells, G. L. & Bradfield, A. L. "Good, you identified the suspect": feedback to eyewitnesses distorts their reports of the witnessing experience. *J. Appl. Psychol.* **83**, 360–376 (1998).
34. Bradfield, A. L., Wells, G. L. & Olson, E. A. The damaging effect of confirming feedback on the relation between eyewitness certainty and identification accuracy. *J. Appl. Psychol.* **87**, 112–120 (2002).
35. Luus, C. A. E. & Wells, G. L. The malleability of eyewitness confidence: co-witness and perseverance effects. *J. Appl. Psychol.* **79**, 714–723 (1994).
36. Garrioch, L. & Brimacombe, C. A. E. Lineup administrators' expectations: their impact on eyewitness confidence. *Law Hum. Behav.* **25**, 299–315 (2001).
37. Shaw, J. S. & McClure, K. A. Repeated postevent questioning can lead to elevated levels of eyewitness confidence. *Law Hum. Behav.* **20**, 629–653 (1996).
38. Morgan, C. A. *et al.* Accuracy of eyewitness memory for persons encountered during exposure to highly intense stress. *Int. J. Law Psychiatry* **27**, 265–279 (2004).
39. Morgan, C. A., Southwick, S. M., Hazlett, G. A. & Loftus, E. F. Misinformation can influence memory for recently experienced, highly stressful events. *Int. J. Law Psychiatry* **36**, 11–17 (2013).
40. Loftus, E. F. & Burns, T. E. Mental shock can produce retrograde amnesia. *Mem. Cognit.* **10**, 318–323 (1982).
41. Christianson, S. & Loftus, E. F. Memory for traumatic events. *Appl. Cogn. Psychol.* **1**, 225–239 (1987).
42. Stark, S. M., Yassa, M. A., Lacy, J. W. & Stark, C. E. L. A task to assess behavioral pattern separation (BPS) in humans: data from healthy aging and mild cognitive impairment. *Neuropsychologia* http://dx.doi.org/10.1016/j.neuropsychologia.2012.12.014 (2013).
43. Holst, V. F. & Pezdek, K. Scripts for typical crimes and their effects on memory for eyewitness testimony. *Appl. Cogn. Psychol.* **6**, 573–587 (1992).
44. Hebb, D. O. *The Organization of Behavior* (John Wiley & Sons Inc., 1949).
45. Bliss, T. V. & Lømo, T. Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path. *J. Physiol.* **232**, 331–356 (1973).
46. Martin, S. J. & Morris, R. G. New life in an old idea: the synaptic plasticity and memory hypothesis revisited. *Hippocampus* **12**, 609–636 (2002).
47. Nicoll, R. A. & Roche, K. W. Long-term potentiation: peeling the onion. *Neuropharmacology* http://dx.doi.org/10.1016/j.neuropharm.2013.02.010 (2013).
48. Redondo, R. L. & Morris, R. G. Making memories last: the synaptic tagging and capture hypothesis. *Nature Rev. Neurosci.* **12**, 17–30 (2011).
49. McClelland, J. L., McNaughton, B. L. & O'Reilly, R. C. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychol. Rev.* **102**, 419–457 (1995).
50. Pastalkova, E. *et al.* Storage of spatial information by the maintenance mechanism of LTP. *Science* **313**, 1141–1144 (2006).
51. Volk, L. J., Bachman, J. L., Johnson, R., Yu, Y. & Huganir, R. L. PKM-ζ is not required for hippocampal synaptic plasticity, learning and memory. *Nature* **493**, 420–423 (2013).
52. Nader, K. & Einarsson, E. O. Memory reconsolidation: an update. *Ann. NY Acad. Sci.* **1191**, 27–41 (2010).
53. Hardt, O., Einarsson, E. O. & Nader, K. A bridge over troubled water: reconsolidation as a link between cognitive and neuroscientific memory research traditions. *Annu. Rev. Psychol.* **61**, 141–167 (2010).
54. McCloskey, M. & Zaragoza, M. Misleading postevent information and memory for events: arguments and evidence against memory impairment hypotheses. *J. Exp. Psychol. Gen.* **114**, 1–16 (1985).
55. Berman, D. E. & Dudai, Y. Memory extinction, learning anew, and learning the new: dissociations in the molecular machinery of learning in cortex. *Science* **291**, 2417–2419 (2001).
56. Kim, J. J. & Fanselow, M. S. Modality-specific retrograde amnesia of fear. *Science* **256**, 675–677 (1992).
57. Wiltgen, B. J. & Silva, A. J. Memory for context becomes less specific with time. *Learn. Mem.* **14**, 313–317 (2007).
58. Winocur, G., Moscovitch, M. & Sekeres, M. Memory consolidation or transformation: context manipulation and hippocampal representations of memory. *Nature Neurosci.* **10**, 555–557 (2007).

59. Wiltgen, B. J. *et al.* The hippocampus plays a selective role in the retrieval of detailed contextual memories. *Curr. Biol.* **20**, 1336–1344 (2010).
60. Ramirez, S. *et al.* Creating a false memory in the hippocampus. *Science* **341**, 387–391 (2013).
61. Iordanova, M. D. & Honey, R. C. Generalization of contextual fear as a function of familiarity: the role of within- and between-context associations. *J. Exp. Psychol. Anim. Behav. Process* **38**, 315–321 (2012).
62. Iordanova, M. D., Good, M. & Honey, R. C. Retrieval-mediated learning involving episodes requires synaptic plasticity in the hippocampus. *J. Neurosci.* **31**, 7156–7162 (2011).
63. Kuhl, B. A., Shah, A. T., DuBrow, S. & Wagner, A. D. Resistance to forgetting associated with hippocampus-mediated reactivation during new learning. *Nature Neurosci.* **13**, 501–506 (2010).
64. Okado, Y. & Stark, C. E. Neural activity during encoding predicts false memories created by misinformation. *Learn. Mem.* **12**, 3–11 (2005).
65. Slotnick, S. D. & Schacter, D. L. A sensory signature that distinguishes true from false memories. *Nature Neurosci.* **7**, 664–672 (2004).
66. Stark, C. E., Okado, Y. & Loftus, E. F. Imaging the reconstruction of true and false memories using sensory reactivation and the misinformation paradigms. *Learn. Mem.* **17**, 485–488 (2010).
67. Johnson, M. K. & Raye, C. L. Reality monitoring. *Psychol. Rev.* **88**, 67–85 (1981).
68. Gutchess, A. H. & Schacter, D. L. The neural correlates of gist-based true and false recognition. *Neuroimage* **59**, 3418–3426 (2012).
69. Rissman, J., Greely, H. T. & Wagner, A. D. Detecting individual memories through the neural decoding of memory states and past experience. *Proc. Natl Acad. Sci. USA* **107**, 9849–9854 (2010).
70. Roozendaal, B. & McGaugh, J. L. Memory modulation. *Behav. Neurosci.* **125**, 797–824 (2011).
71. Andreano, J. M. & Cahill, L. Glucocorticoid release and memory consolidation in men and women. *Psychol. Sci.* **17**, 466–470 (2006).
72. Kirschbaum, C., Wolf, O. T., May, M., Wippich, W. & Hellhammer, D. H. Stress- and treatment-induced elevations of cortisol levels associated with impaired declarative memory in healthy adults. *Life Sci.* **58**, 1475–1483 (1996).
73. Boujabit, M., Bontempi, B., Destrade, C. & Gisquet-Verrier, P. Exposure to a retrieval cue in rats induces changes in regional brain glucose metabolism in the amygdala and other related brain structures. *Neurobiol. Learn. Mem.* **79**, 57–71 (2003).
74. Buss, C., Wolf, O. T., Witt, J. & Hellhammer, D. H. Autobiographic memory impairment following acute cortisol administration. *Psychoneuroendocrinology* **29**, 1093–1096 (2004).
75. Kuhlmann, S., Piel, M. & Wolf, O. T. Impaired memory retrieval after psychosocial stress in healthy young men. *J. Neurosci.* **25**, 2977–2982 (2005).
76. Otgaar, H., Candel, I., Merckelbach, H. & Wade, K. A. Abducted by a UFO: prevalence information affects young children's false memories for an implausible event. *Appl. Cogn. Psychol.* **23**, 115–125 (2009).
77. Howe, M. L., Candel, I., Otgaar, H., Malone, C. & Wimmer, M. C. Valence and the development of immediate and long-term false memory illusions. *Memory* **18**, 58–75 (2010).
78. Payne, J. D. *et al.* The role of sleep in false memory formation. *Neurobiol. Learn. Mem.* **92**, 327–334 (2009).
79. Geiselman, R. E. *et al.* Enhancement of eyewitness memory: an empirical evaluation of the cognitive interview. *J. Police Sci. Administr.* **12**, 74–80 (1984).
80. Godden, D. R. & Baddeley, A. D. Context-dependent memory in two natural environments: on land and underwater. *Br. J. Psychol.* **66**, 325–331 (1975).
81. Malpass, R. S. & Devine, P. G. Eyewitness identification: lineup instructions and the absence of the offender. *J. Appl. Psychol.* **66**, 482–489 (1981).
82. Steblay, N. K., Dysart, J. E. & Wells, G. L. Seventy-two tests of the sequential lineup superiority effect: a meta-analysis and policy discussion. *Psychol. Public Policy Law* **17**, 99–139 (2011).
83. Steblay, N., Dysart, J., Fulero, S. & Lindsay, R. C. L. Eyewitness accuracy rates in sequential and simultaneous lineup presentation: a meta-analytic comparison. *Law Hum. Behav.* **25**, 459–474 (2001).
84. Lindsay, R. C. L., Mansour, J. K., Beaudry, J. L., Leach, A.-M. & Bertrand, M. I. Sequential lineup presentation: patterns and policy. *Legal Criminol. Psychol.* **14**, 13–24 (2009).
85. Allport, G. W. & Postman, L. *The Psychology of Rumor* (Henry Holt and Company, 1947).
86. Hartley, J. Note-taking research: resetting the scoreboard. *Bull. Br. Psychol. Soc.* **36**, 13–14 (1983).
87. Luria, A. R. *The Mind of a Mnemonist: a Little Book About a Vast Memory* (Harvard Univ. Press, 1987).
88. Woocher, F. D. Did your eyes deceive you? Expert psychological testimony on the unreliability of eyewitness identification. *Stanford Law Rev.* **29**, 969–1030 (1977).
89. Brigham, J. C., Maass, A., Snyder, L. D. & Spaulding, K. Accuracy of eyewitness identifications in a field setting. *J. Personal. Social Psychol.* **42**, 673–681 (1982).
90. Yuille, J. C. & Cutshall, J. L. A case study of eyewitness memory of crime. *J. Appl. Psychol.* **71**, 291–301 (1986).
91. Morgan, C. A. *et al.* Hormone profiles in humans experiencing military survival training. *Biol. Psychiatry* **47**, 891–901 (2000).

Competing interests statement
The authors declare no competing financial interests.

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